

ART. XXIII.—*On the systematic position of the species of Squalodon and Zeuglodon described from Australia and New Zealand.*

By T. S. HALL, M.A., D.Sc.

(University of Melbourne).

(With Plate XXXVI.)

[Read 13th October, 1910.]



McCoy in 1864¹ described *Squalodon wilkinsoni* from the tertiary polyzoal limestone of Cape Colony. The species was founded on a single molar tooth in a good state of preservation. In 1866² the species was again characterised on the same tooth, but in less rigid terms, and the essay containing the description was reprinted in the following year³. In it McCoy referred the species to "*Squalodon* or *Phocodon*," the names being synonymous.

In 1875⁴ the same author published a description of the same tooth for the fourth time, and gave a good figure. Four years later⁵ he figured another tooth of a simpler character, and referred it to the same species as one of the "anterior" teeth. This specimen came from Waurn Ponds, and the same quarry has also yielded a fragment of a molar and an additional probable incisor. These are, it would seem, all correctly referred to the same species.

Still later⁶ E. B. Sanger described a similar molar from beds of the same age at Wellington, on the Murray River in South Australia. To this he gave the name *Zeuglodon harwoodi*. I have been unable to trace this specimen, which has apparently disappeared, and Mr. J. J. Fletcher, the secretary of the Linnean Society, is unable to give me any information about it. This

1 Geol. Mag., v. 4; 1864, p. 145, pl. S, f. 1.

2 Exhibition Essays, 1866.

3 Annals and Mag. Nat. Hist., v. 20; 1867, p. 191.

4 Prodr. Pal. Victoria; decade 2, 1875, pl. ii., ff. 1-1d.

5 *Ib.*, Dec. 6, 1879, pl. 55, ff. 3-3b.

6 Proc. Linn. Soc. N.S. Wales, v. 5, 1881, pp. 298-300, wdct.

is unfortunate, as the description gave no account of the surface of the tooth, which the figure appears to indicate as smooth. As regards the form of the tooth, it seems to have relatively much more slender roots than M'Coy's type molar, and in the size and arrangement of its cusps it resembles a specimen from Mount Gambier, figured below. I think that this form of tooth must indicate an animal quite distinct from M'Coy's, as such a marked difference in the proportionate size of the roots would probably be correlated with differences in the strength of the jaws.

As regards New Zealand, we find two records of the serrated teeth characteristic of Zeuglodonts and Squalodonts. The first is by Sir James Hector, who in 1881¹ described *Kekenodon onamata*² as a Zeuglodont. He had fragments of a lower jaw and of ten imperfect teeth, but figures only the latter. In 1888 J. W. Davis founded *Squalodon serratus* on a tooth partly hidden by matrix. He says that it closely resembles that described by M'Coy as *S. wilkinsoni*, but differs in the number of lateral denticles or cones.

This is, of course, a variable feature depending on the position of the tooth in the series. I would doubtfully put this under the synonymy of Sanger's species, *Z. harwoodi*. Besides these records a Squalodont tooth was found some years ago at Table Cape by Prof. Baldwin Spencer, and was handed over to Prof. Ralph Tate at the time. The specimen is in the Adelaide University Museum, and I have to thank Mr. W. Howchin for an opportunity of examining it. It bears a label with a *MS* name of the late Professor Tate's, namely, *Zeuglodon brevicuspidatus*. In the same drawer was found a paper with the following note in Tate's handwriting:—" *Zeuglodon s.*, distinguished from *Z. Harwoodi* and *Z.* [blank] (Alabama) by its small cusps and deep angular rugosities, also from *Squalodon Wilkinsoni* by the same characters apart from its prob. diff. generic location."

As Mr Howchin tells me, it is not known whether the above description was intended to apply to the present specimen. The probabilities are, I think, that it was so.

¹ Trans. and Proc. N. Zealand Inst., v. 13, 1881, p. 435, pl. 18.

² Zittel in his Handbook misspells both the generic and specific name, and gives a puzzling variant of *S. wilkinsoni*. The errors are repeated in the French edition.

The specimen consists of merely partly hollow crown packed with the characteristic large, well-rounded quartz grains of the basal beds at Table Cape. A reference to the figure will show the obliquity of the crown and the presence of two large cusps on the front edge, and three on the hind one. This points in the direction of the Squalodonts rather than of the Zeuglodonts. The crown is higher and narrower than M'Coy's type, and thus approaches the more anterior tooth figured from Spring Creek. Though the root is absent I am of opinion that the Table Cape specimen is conspecific with M'Coy's species, and is more anterior than his type.

The Victorian National Museum has a fine molar from the Mount Gambier polyzoal limestone, which has been referred to above.

I have what appears to be a premolar from the Middle Spring Creek beds, which I found several years ago. These are all the records or material of which I can find trace. No other bones belonging to these whales have been found unless some of those recorded as "Cetotolites" may be so referred.

Hector's *Kekenodon* in some ways stands apart from all the others. The crowns of the teeth as compared with the roots are much smaller. The surfaces of the crowns are stated by Hector to be fluted and polished. Casts of some of the teeth are in the National Museum here, but the flutings are not shown, and cannot, I think, have been as pronounced as in *S. wilkinsoni*.

We have then three species, which, as I shall attempt to show, it would seem advisable to refer to as many distinct genera.

The separation of the Zeuglodontidae and the Squalodontidae rests fundamentally on the formation of the skull, the Zeuglodonts being more generalised, or archaic, in that the anterior nares are far forward, the nasals being large. Both families are usually grouped with the Cetacea, the latter as a distinct sub-order, Archaeoceti or Zeuglodontes. The Squalodonts with small nasal bones, and an anterior nasal opening on the top of the head, are grouped with the Odontoceti under the family Squalodontidae.

The only suggested difference shown by the teeth in the two families is, as has been pointed out by several observers, that

the cusps on the anterior cutting-edges in Squalodonts are less conspicuous than those on the hind edges¹.

There seems to be great variation in the ornament on the teeth, though perhaps imperfect figures and descriptions may mislead us here, as very few authors pay much attention to the point.

Andrews² says that in *Prozeuglodon* the enamel at the base of the crown is raised into fine ridges. In *Z. isis* he describes the surface, especially that of the inner side of the crown, as covered with anastomosing ridges, which do not run on to the serrations of the posterior border. Carus³ appears to figure the teeth of *Z. hydrarchos* as smooth. Gaudry⁴ figures *S. grateloupei* as roughly ridged, but his illustration is only a woodcut. *Zeuglodon cetoides* he figures as quite smooth, but the drawing is, he says, from a cast. Koch⁵ shows *Z. macrospondylus* from Alabama as fluted. Lydekker⁶ shows the teeth of *Z. caucasicus* (type of *Microzeuglodon*, von Stromer) as smooth, *Rhizoprion bariense*. Jourdan's figures⁷ show with a few coarse longitudinal grooves. Owen⁸ shows the teeth of *Z. cetoides* as smooth. Casts of the teeth of *Z. cetoides* in the National Museum show the molars and canines to be smooth and polished. Van Beneden's "Description des ossements fossiles des environs d'Anvers" and the "Ostéographie des cetacés" by Gervais and van Beneden are unfortunately not in Melbourne, but the latter author⁹ in speaking of *S. antverpiensis* says the crowns of the teeth are coated with enamel covered with grooves separated from one another by an equal space of 1 mm. and his figure (pl. 1) shows a tooth ornamented like M'Coy's type of *S. wilkinsoni*. He gives further particulars as to the surface of the teeth which show their resemblance to M'Coy's species and points out that the teeth of *Zeuglodon* are all remarkable by the number and

1 e.g., Lydekker, 1893, p. 9.

2 Andrews, 1906, p. 255.

3 Carus, pls. 39A, 39B.

4 pp. 30 and 38.

5 Koch, pl. 7.

6 Lydekker, 1892.

7 Jourdan, pl. 10.

8 Owen, pl. 7.

9 Van Beneden, 1876, p. 476.

form of the crenulations and the two edges always resemble one another more than in *Squalodons*. The same author in another paper¹ says that in *S. servatum* the teeth are coated with a thick layer of enamel the surface of which is always "striée*ou guillochée." For the latter word I can get no satisfactory meaning. "Engine-turning" or the geometric interlacing of curved lines does not seem applicable to any ornament described or figured elsewhere.

Similar references could be multiplied but the quotations are sufficient to show that ornament alone is not sufficient to fix the generic position of an unknown tooth.

An additional character common to the Northern Zeuglodonts and Squalodonts is the complete separation of the divergent roots of the molar teeth. This character is not shown in any of the corresponding teeth in the Southern forms as far as is known. In *Prosqualodon* from the Chubut deposits of Argentina Lydekker¹ states that in the molariform teeth the fangs have coalesced, but are separated by a deep groove, and he gives a text-figure showing this feature. True² says the teeth of *Prosqualodon* which he examined did not exhibit the amount of divergence that Lydekker figured. Sanger³ says that the two fangs of his species are connected by an isthmus. The same character of the coalescence of the fangs is shown in McCoy's type, in the specimens from Mount Gambier and from Spring Creek.

The fusion of the roots seems to be of sufficient importance to separate the Southern forms from *Squalodon* and *Zeuglodon* alike, and as Lydekker's *Prosqualodon* shows the fusion and is undoubtedly Squalodont it will be found advisable, I think, to refer the Australian species to the same family of short-beaked forms.

In the case of *Kekenodon* there is a peculiarity. The roots are united in most of the teeth, but in some at least they run parallel, but not quite in contact. Their passage towards complete union has not advanced as far as in the Australian species. One tooth, moreover, has a third root, a feature which is more ar-

1 Lydekker, 1899, p. 921.

2 True, 1910, p. 450.

3 Sanger, 1881, p. 298.

chaic than anything found in *Squalodon*, but occurs in the Fayum *Prozeuglodon*.¹ This character is regarded by Andrews as of generic value.

The differences which exist in the teeth are, I think, of sufficient importance to enable us to separate three genera which may be referred to the Squalodontidae and may be defined as follows:—

KEKENODON, Hector.

Teeth with massive roots, three or four times as long as the crown. Roots usually united for their whole length, and in every case never widely separated. A third root in some teeth. Lateral cusps on the crowns strong and freely projecting. Surface of crowns, according to Hector, fluted.

Only species *Kekenodon onamata*, Hector.

PARASQUALODON, gen. nov.

Roots of molariform teeth slightly more than twice the length of the crown. Roots united throughout their length and in some teeth slightly hooked at the end. Lateral cusps on the teeth rather small. Surface of crown covered with cord like the tip of the tooth. Ridges roughened with small rounded prominences. In the (?) premolar figured (Pl. XXXVI., Fig. 3) the sharp edges of the teeth are slightly serrated, the serrations varying in size from these prominences to distinct, though small, cusps. Anterior teeth with the same cordlike ornament, but without lateral cusps, and from the same horizon, are provisionally referred to the same genus and species.

Only species *Parasqualodon wilkinsoni*, M'Coy.

Metasqualodon, n. g.

Roots of molariform teeth slender and only a little longer than the height of the crown, the two fangs connected by a thin "isthmus" much as figured by Lydekker in *Prosqualodon*, but the fangs more nearly approaching one another. The material does not inform us as to whether the fangs were connected

¹ Andrews, p. 251.

throughout their length by the isthmus, or whether they projected freely beyond it. Lateral cusps rather large. Ornament as in *Parasqualodon*.

Only species *Metasqualodon harwoodi*, Sanger.

In discussing the affinities of *Prosqualodon*, Lydekker says that in the structure of the nasals the South American genus is more generalised than *Squalodon*, while in the character of the teeth it is more specialised. As we know only the teeth of our Australasian genera, and these imperfectly, we cannot say whether or not they were in advance of the specialisation of the skull.

Geologists are as yet undecided as to the age of the Patagonian tertiaries. Those in the United States, and most of those in Europe, refer to the Santa Cruz beds which yielded *Prosqualodon* to early miocene or perhaps oligocene. Von Ihering, who has spent many years on the task, and is familiar with the recent mollusca of South America, still fights vigorously for their eocene age, and is, I think, working on correct lines.

The New Zealand *Kekenodon* is said by Hector to be eocene, but the matter is still in doubt. As regards the beds in Southern Australia which have yielded Squalodonts, opinions vary between eocene, oligocene and miocene. At present those which have yielded *Prosqualodon* are spoken of merely as Janjukian. The polyzoal limestone of Mount Gambier is, of course, practically devoid of mollusca, and its relationships are consequently not easy to settle, but they appear to lie rather with Muddy Creek, which is Balcombian, than with Janjukian. The beds of the Murray River cliffs, whence Sanger's type came, are generally regarded as Janjukian, but variations may occur in such a great range of outcrop.

There are differences of opinion as to the sequence of these two subdivisions of the Barwonian system, my view being that Janjukian is the older.

LITERATURE.

- Andrews, C. W. (1906.—Descriptive catalogue of the tertiary vertebrata of the Fayum, Egypt, etc. British Museum.
- Carus, G. C., 1850.—Das Kopfskelet des Zeuglodon hydrarchos. Nov. Act. Ac. Caes. v. 22, pt. 2, pl. 39a, 39b.

- Davis, J. W., 1888.—On fossil fish remains from New Zealand. *Sci. Trans. Roy. Dublin Soc.*, S. 2, v. 4.
- Gaudry, A., 1878.—Les enchainements du monde animal dans les temps géologiques.
- Hector, J., 1881.—Tr. and Proc. N. Zealand Inst. v. 13, p. 435, pl. xviii.
- Jourdan, 1861.—*Ann des Sci. Nat.*, 4 S. v. 16, p. 368, pl. 10.
- Koch, A., 1851.—Das Skelet des Zeuglodon macrospondylus. *Naturw. Abhandl.* v. 4, pp. 53-64, pl. 7.
- Lydekker, R., 1892.—On Zeuglodont and other Cetacean remains from the Tertiary of the Caucasus. *Proc. Zool. Soc.*, p. 558, pl. 36-38.
- Lydekker, R., 1893.—Contributions to a knowledge of the fossil vertebrates of Argentina. *Ann. Mus. La Plata. Pal. Argentina* v. 2.
- Lydekker, R., 1899.—On the skull of a shark-toothed dolphin from Patagonia. *Proc. Zool. Soc.*, p. 919
- M'Coy, F., 1864.—*Geolog. Mag.* v. 4, p. 145, pl. 8.
- M'Coy, F., 1867.—*Ann. Mag. Nat. Hist.* v. 20, p. 191.
- M'Coy, F., 1867.—*Intercolonial Exhibition, Essays.*
- M'Coy, F., 1875.—*Prod. Palaeont. Victoria*, Dec. 2, pl. 11.
- M'Coy, F., 1879.—*Id.*, Dec. 6, pl. 55.
- Owen, R., 1843.—*Tr. Geo. Soc. Lond.* v. 6, p. 69, pls. 7-9.
- Sanger, E. B., 1881.—*Proc. Linn. Soc., N.S. Wales*, p. 298, text. fig.
- True, F. W., 1908.—*Proc. Am. Phil. Soc.* v. 47.
- True, F. W., 1910.—*Smithsonian Misc. Coll.* v. 52, p. 441.
- van Beneden, P. J., 1864.—*Mém. Ac. Roy. Belg.*, v. 34.
- van Beneden, P. J., 1876.—*Bull. Ac. Roy. Belg.*, 2. S. v. 41, p. 474.
- Note.*—Ostéographie des Cétacés vivantes et fossiles, by van Beneden and Gervais, and the former author's Description des ossements fossiles des environs d'Anvers, in *Ann. Mus. H.N. Belgique* are not available in Melbourne.

DESCRIPTION OF PLATE XXXVI.

Fig. 1.—Incisor of (?) *Parasqualodon wilkinsoni*, Waurn Ponds. (Coll. Nat. Mus.).



1



2



3



4



5



6



A

7



B

- Fig. 2.—Incisor of *P. wilkinsoni*, Waurin Ponds. (Coll. Nat. Mus.) Figured by M^cCoy.
- 3.—Premolar of *P. wilkinsoni*, Spring Creek. (Coll. T. S. Hall).
- 4.—Molar of *P. wilkinsoni*, Table Cape. (Coll. Geolog. Dept. Adelaide Univ.).
- 5.—Molar of *P. wilkinsoni*, Castle Cove, Cape Otway. (Coll. Nat. Mus.) M^cCoy's type.
- 6.—Molar of *Metasqualodon harwoodi*, Mount Gambier. (Coll. Nat. Mus.).
- 7.—(A) Molar of *M. harwoodi*. After Sanger.
(B) Transverse section of roots of molar of *M. harwoodi*, showing their union. After Sanger.
(The figures are all about natural size).

